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Relationships among forage chemistry, rumination and retention time with intake and digestibility of hay by goats☆,☆☆

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Abstract

Eight species of forage, a cool-season perennial (tall fescue (*Festuca arundinacea*)) and annual grass (winter wheat (*Triticum aestivum*)), four warm-season perennial grasses (caucasian (*Bothriochloa caucasica*), plains (*B. ischaemum*), old world bluestem, bermudagrass (*Cynodon dactylon*), and eastern gamagrass (*Tripsacum dactyloides*)), a warm season annual (crabgrass (*Digitaria sanguinalis*)) and a perennial legume (alfalfa (*Medicago sativa*)), were each cut at two or three maturities to provide a wide array of quality difference ($n = 20$). Twenty wether goats (*Capra hicus*) were fed the hays in four different trials using an incomplete block design so that four different goats received each hay. Alfalfa produced the highest (25 g kg^{-1} body weight (BW)) and wheat the lowest (13.6 g kg^{-1} BW) organic matter (OM) intake. A number of the grasses provided less than 20 g kg^{-1} BW OM intake. Digestion of OM was also highest for alfalfa (>715 g kg^{-1}) and lowest for bermudagrass (508 g kg^{-1}). All measures and expressions of intake and digestibility were better related to ruminating and retention time than to forage chemistry, with the exception of crude protein digestibility. The best equations for predicting intake included a combination of mean retention time and forage acid detergent fiber (ADF) content (reciprocal and quadratic); that for digestibility included permanganate lignin (reciprocal), and the quadratic for ruminating and retention time. Equations for predicting the constraint on intake and digestible organic matter intake produced higher r^2 than those for either intake or digestibility. Digestibility of ADF and neutral detergent fiber (NDF) were poorly predicted with either chemistry ($r^2 \leq 0.20$), or ruminating time ($r^2 = 0.43$), but combinations of permanganate lignin content of NDF, retention and ruminating time produced reasonable equations.
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Keywords: Intake; Digestibility; Rumination time; Retention time; Forage chemistry

1. Introduction

Quality of forages include their limitations to be consumed and digested (Coleman et al., 1999). Since measurement of both intake and digestibility is expensive and laborious, various attempts have been made to predict nutritive potential from forage chemistry and other characteristics. While many axioms have been developed concerning the relationships of forage chemistry, many of the these axioms or conventional

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wisdom have not proven reliable (Moore and Coleman, 2001). The processes governing digestibility are primarily defined by the forage being fed, whereas those governing intake are functions of the forage and the animal as impacted by its environment. Because the variability among animals given the same feed is less variable for digestibility (∼5% coefficient of variation (CV)) than for intake (10–20% CV), digestibility is usually predicted with greater precision than intake (Minson, 1990; Moore, 1994; Coleman et al., 1999). Yet, intake has been suggested the more important parameter for estimating forage quality and animal performance (Minson, 1990; Coleman et al., 1999).

Balch (1969) demonstrated the efficacy of rumination time in the processing of forage and its importance to the limitations forages impose on their intake and processing by the ruminant. The integration of the concepts of passage and digestion rate with intake and extent of digestion have been the subject of many modeling efforts (Waldo et al., 1972), but rarely measured in a single experiment over a wide range of forages. We initiated this research to determine the relationships among forage chemistry, ruminating behavior, digesta retention time, dry matter (DM) intake, and nutrient digestibility of a broad range of hay types, species and maturity.

2. Materials and methods

Twenty hays were collected that represented eight different forage species. Each forage species was cut at two or three maturities. Species were selected to provide variation in plant type and included a cool-season perennial (tall fescue (*Festuca arundinacea*)) and annual grass (winter wheat (*Triticum aestivum*)), four warm-season perennial grasses (caucasian (*Bothriochloa caucasica*) and plains (*B. ischaemum*) old world bluestem, bermudagrass (*Cynodon dactylon*), and eastern gamagrass (*Tripsacum dactyloides*)), a warm season annual (crabgrass (*Digitaria sanguinalis*)) and a perennial legume (alfalfa (*Medicago sativa*)). Each hay was sun cured, compressed into conventional rectangular bales (∼25 kg) and stored in a barn before feeding. Hay description and maturity at harvest are shown in Table 1.

Table 1
Chemical composition of hays fed to goats (mean ± S.E. for each hay)

Species	Maturity	Type[a]	Organic matter	Crude protein ($g\,kg^{-1}$ DM)	Neutral detergent fiber	Acid detergent fiber	Permanganate lignin ($g\,kg^{-1}$ NDF)
Alfalfa	Early bloom	LEG	888.3 ± 10.9	211.1 ± 6.4	426.5 ± 54.9	286.6 ± 33.9	146.9 ± 30.3
Alfalfa	Prebloom	LEG	892.8 ± 7.7	202.8 ± 17.0	464.0 ± 50.7	351.9 ± 28.3	153.4 ± 46.1
Bermudagrass	4 weeks	WSP	914.2 ± 8.7	68.5 ± 4.4	696.1 ± 33.5	377.6 ± 15.6	95.9 ± 15.7
Bermudagrass	8 weeks	WSP	923.5 ± 4.5	96.7 ± 8.3	754.8 ± 25.8	440.0 ± 6.3	110.5 ± 9.6
Bermudagrass	Mature	WSP	911.8 ± 2.3	81.0 ± 8.4	728.3 ± 44.5	391.8 ± 9.3	89.4 ± 9.3
Crabgrass	Boot	WSA	917.8 ± 6.3	89.9 ± 5.9	645.2 ± 8.3	380.1 ± 23.4	91.0 ± 10.7
Crabgrass	Mature	WSA	930.0 ± 4.4	84.5 ± 10.3	672.2 ± 9.3	400.9 ± 10.0	107.5 ± 7.0
Crabgrass	Vegetative	WSA	903.8 ± 5.7	101.0 ± 6.7	628.2 ± 37.6	374.0 ± 52.3	104.2 ± 15.5
Eastern gamagrass	Boot	WSP	915.2 ± 5.8	72.4 ± 2.9	724.8 ± 25.9	409.0 ± 20.4	91.6 ± 16.0
Eastern gamagrass	Early bloom	WSP	926.6 ± 3.0	52.1 ± 5.6	752.5 ± 22.8	435.9 ± 13.1	94.2 ± 4.3
Eastern gamagrass	Mature	WSP	931.5 ± 7.4	63.4 ± 11.8	742.9 ± 24.9	433.0 ± 20.9	94.7 ± 21.9
Fescue	Early bloom	CSP	921.4 ± 16.7	136.8 ± 15.4	619.0 ± 127.4	348.9 ± 49.7	87.4 ± 16.1
Fescue	Mature	CSP	934.4 ± 5.9	67.7 ± 9.5	758.8 ± 9.8	463.3 ± 10.7	101.4 ± 10.1
Fescue	Soft dough	CSP	920.5 ± 1.8	96.0 ± 3.4	709.1 ± 14.9	407.2 ± 25.4	91.3 ± 21.2
Caucasian bluestem	Early bloom	WSP	889.6 ± 5.8	87.5 ± 10.3	679.5 ± 52.5	415.1 ± 27.0	119.3 ± 40.3
Caucasian bluestem	Late bloom	WSP	919.7 ± 3.3	65.8 ± 5.7	703.1 ± 17.0	433.3 ± 38.7	85.2 ± 23.3
Plains bluestem	Early bloom	WSP	901.7 ± 8.0	80.0 ± 4.6	726.2 ± 17.7	422.5 ± 13.2	66.1 ± 9.4
Plains bluestem	Late bloom	WSP	908.2 ± 4.6	75.2 ± 6.0	739.1 ± 16.3	457.5 ± 29.1	91.5 ± 15.2
Wheat	Dough	CSA	912.0 ± 5.2	83.3 ± 8.8	634.8 ± 26.6	378.1 ± 15.2	91.3 ± 6.8
Wheat	Milk	CSA	927.0 ± 13.9	71.2 ± 7.6	763.6 ± 24.0	503.9 ± 8.1	100.2 ± 36.6

[a] LEG, legume; WSP, warm season perennial; WSA, warm season annual; CSP, cool season perennial; CSA, cool season annual.

About 100 kg of each hay was passed through a hammermill with a 3.8 cm screen to reduce particle size to approximately 2.5 cm in length. Alfalfa was ground without a screen to reduce leaf shatter. The processed hay was stored in wool bags while the feeding trials were being conducted.

Twenty yearling Alpine wether goats (average body weight = 28.5 kg) were selected and placed in wooden crates suitable for separation of feces and urine. Each goat was randomly assigned to one of the hay sources for trial 1. They were offered sufficient amounts of the respective hays at 08:00 h each day to achieve refusal of 10%. After 7 days for diet adaptation (10 days for trial 1), intake was recorded as feed consumed during days 8 through 14, and feces were collected from days 11 through 15. On day 10, each animal was given 200 g of their respective hay marked with $YbCl_3$ according to Ellis et al. (1994).

Samples of hay, refusals and feces were dried at 65 °C and ground to pass a 1 mm screen, and were subsequently analyzed for DM, ash, and crude protein (CP) according to AOAC (1984) and for neutral detergent fiber (NDF), acid detergent fiber (ADF) and permanganate lignin (PML) according to Goering and Van Soest (1970). Chemical composition of the refusals were used to adjust for any selectivity that may have occurred. Daily DM and nutrient intake and nutrient digestibility were calculated for each animal. Yb content of feces was determined by atomic absorption spectroscopy by the method of Hart and Polan (1984). Rate of passage was determined by regression of fecal Yb concentration on time from dosing using the NLIN procedure of SAS (1990). The model was the two-compartment, age independent model described by Ellis et al. (1994).

During the fourth day of collection, observations were made of each animal every 5 min for 24 h using methods described by Woodford and Murphy (1988). At each 5 min interval, the activity of each goat was recorded as eating, ruminating, standing, lying or drinking. Only rumination time was used in this report.

Following the first trial, the goats were re-randomized to a different hay, and the procedures were repeated. They were repeated for a third and fourth trial so that each hay was fed to four different goats during the four trials. All 20 hays were fed in each trial so that only goat and trial (period) were confounded. The experimental design was a balanced incomplete block, although comparison of hay was not a primary objective of the experiment, but to develop relationships among hay characteristics, animal eating behavior, and hay intake and digestibility. The REG procedure (SAS, 1990) with stepwise option was used to develop equations to predict different expressions of intake and nutrient digestibility using forage chemistry, rumination time, and passage rate. Non-linearity of relationships were accounted for by including reciprocals and quadratic transformations of the independent variables (hay chemistry and rumination time).

3. Results

3.1. Chemical and nutritive description of hays

Crude protein was highest in alfalfa (average 206 g kg^{-1}) and lowest in warm-season perennial grasses (<80 g kg^{-1} for 4 weeks bermudagrass, all eastern gamagrasses, and late bloom caucasian and plains bluestem, and wheat hay cut in milk stage; Table 1). Nutritionists generally regard 70–80 g kg^{-1} as the minimum CP for adequate rumen microflora function (Minson, 1990). Perennial grasses contained the highest levels of NDF (average 725 g kg^{-1} for warm-season and 696 g kg^{-1} for cool-season perennials). Alfalfa contained lower levels of ADF (319 g kg^{-1}) than grasses in general (413 g kg^{-1}), but some immature grasses (e.g. fescue and crabgrass) were similar in ADF content as mature alfalfa.

Organic matter digestibility (OMD) ranged from a low of 422 g kg^{-1} for mature fescue to 657 g kg^{-1} for early bloom alfalfa (Table 2), with standard deviations (S.D.) among animals ranging from 2.9 to 66.3 g kg^{-1}. Perennial grasses clustered about 550 g kg^{-1} OMD, much as would be expected. Digestibility of NDF and ADF ranged from a low of 430 and 447 g kg^{-1} for mature fescue to a high of 652 and 661 g kg^{-1} for early bloom plains bluestem, respectively.

Overall true digestibility of protein was 860 g kg^{-1} (Fig. 1), slightly lower than that reported by Van Soest (1982, p. 50) for sheep and goats (950 g kg^{-1}). The r^2 of 0.99 indicated that with these diverse forages, protein behaved as a true nutritive entity (Lucas Jr. et al., 1961; Van Soest, 1982, pp. 43–46). Metabolic

Table 2
Nutrient total tract digestibility ($g\,kg^{-1}$) and indigestible protein ($g\,kg^{-1}$) of experimental hays (mean ± S.E. for each hay)

Species	Maturity	Organic matter digestibility	Protein digestibility	NDF digestibility	ADF digestibility	Truly indigestible protein[a]
Alfalfa	Early bloom	657.3 ± 55.0	716.2 ± 42.7	581.4 ± 103.6	586.8 ± 59.0	30.7 ± 7.4
Alfalfa	Prebloom	609.9 ± 23.0	714.5 ± 23.9	513.7 ± 59.69	545.4 ± 27.7	28.6 ± 2.0
Bermudagrass	4 weeks	508.0 ± 66.3	463.9 ± 69.3	515.4 ± 52.52	542.2 ± 63.7	7.3 ± 2.1
Bermudagrass	8 weeks	532.5 ± 23.3	535.3 ± 34.0	566.4 ± 31.47	597.1 ± 28.0	15.8 ± 4.0
Bermudagrass	Mature	520.7 ± 30.3	522.5 ± 39.7	527.6 ± 22.57	564.5 ± 25.1	9.6 ± 3.6
Crabgrass	Boot	578.8 ± 60.2	520.9 ± 64.6	586.6 ± 77.71	588.8 ± 76.3	13.8 ± 3.0
Crabgrass	Mature	572.7 ± 23.0	488.4 ± 53.3	581.8 ± 26.11	582.7 ± 13.1	13.9 ± 3.0
Crabgrass	Vegetative	577.7 ± 30.0	504.6 ± 91.0	573.0 ± 15.72	561.7 ± 33.9	20.7 ± 6.3
Eastern gamagrass	Boot	545.9 ± 20.2	471.5 ± 56.4	553.9 ± 34.49	582.8 ± 32.3	9.2 ± 3.3
Eastern gamagrass	Early bloom	586.2 ± 13.5	360.9 ± 93.1	603.8 ± 11.34	637.2 ± 13.2	4.0 ± 3.4
Eastern gamagrass	Mature	546.3 ± 38.6	340.4 ± 148.3	575.0 ± 47.49	608.6 ± 25.6	11.5 ± 4.3
Fescue	Early bloom	630.9 ± 26.2	632.8 ± 37.4	603.7 ± 144.1	649.8 ± 74.1	20.8 ± 1.9
Fescue	Mature	422.3 ± 10.2	359.9 ± 168.2	430.0 ± 28.81	447.6 ± 29.0	13.1 ± 4.4
Fescue	Soft dough	556.2 ± 34.1	582.2 ± 63.9	536.9 ± 100.4	572.5 ± 42.7	11.0 ± 5.5
Caucasian bluestem	Early bloom	581.1 ± 2.9	507.4 ± 49.4	589.2 ± 26.55	589.1 ± 31.3	13.8 ± 3.8
Caucasian bluestem	Late bloom	605.9 ± 34.4	452.7 ± 43.8	625.6 ± 41.72	644.6 ± 28.1	6.9 ± 3.5
Plains bluestem	Early bloom	625.1 ± 38.2	492.0 ± 44.3	652.0 ± 42.5	661.7 ± 54.1	11.5 ± 2.6
Plains bluestem	Late bloom	590.0 ± 21.1	503.2 ± 78.8	622.2 ± 15.59	650.7 ± 22.2	8.0 ± 2.7
Wheat	Dough	569.5 ± 13.5	528.8 ± 19.8	512.5 ± 19.28	529.6 ± 17.2	10.2 ± 3.2
Wheat	Milk	535.9 ± 31.0	418.2 ± 47.3	563.2 ± 49.72	591.6 ± 26.0	12.2 ± 2.1

[a] Calculated by subtracting metabolic fecal protein ($29\,g\,kg^{-1}$; see Fig. 1) from apparent indigestible protein.

fecal protein (MFP; calculated as the intercept) was $29\,g\,kg^{-1}$ of dry matter consumed.

Organic matter intake (Table 3) was highest for the legume hays and lowest for wheat hay cut in the milk stage. OM intake for bermudagrass (4 weeks), fescue (mature) and eastern gamagrass (early bloom) was also quite low, (about $16\,g\,kg^{-1}$ BW). The most mature hay within a species did not always produce the lowest digestibility or intake. Within hay, the S.D. among animals varied from 1.0 to $9.9\,g\,kg^{-1}$ BW which was

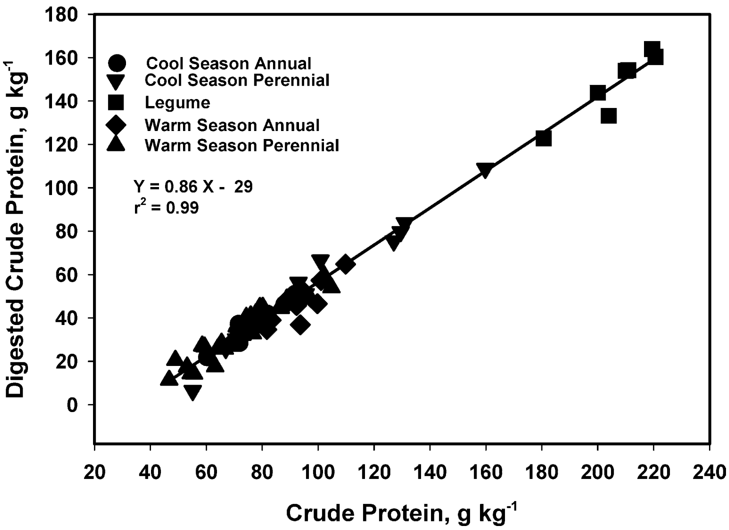

Fig. 1. Relationship of crude protein content and digested crude protein illustrating the ideal nutritive entity (Lucas Jr. et al., 1961).

Table 3
Intake, passage dynamics and chewing behavior of goats consuming experimental hays (mean ± S.E. for each hay)

Species	Maturity	Organic matter intake ($g\,kg^{-1}$ BW)	Digestible organic matter intake ($g\,kg^{-1}$ BW)	Intake constraint g OMI (kg^{-1} MBS)	Passage rate ($g\,g^{-1}\,h^{-1}$)	Rumen mean retention time (h)	Total mean retention time (h)	Rumination time (min)
Alfalfa	Early bloom	24.0 ± 6.8	15.9 ± 5.0	49.3 ± 22.8	0.036 ± 0.012	29.9 ± 11.3	51.8 ± 14.9	322 ± 82
Alfalfa	Prebloom	25.0 ± 4.8	15.2 ± 2.7	54.9 ± 11.0	0.047 ± 0.008	22.1 ± 4.3	47.2 ± 3.5	372 ± 81
Bermudagrass	4 weeks	16.6 ± 9.9	8.8 ± 5.4	108.2 ± 48.8	0.025 ± 0.013	53.3 ± 38.5	86.7 ± 49.4	381 ± 177
Bermudagrass	8 weeks	19.2 ± 1.6	10.2 ± 0.8	91.3 ± 7.8	0.030 ± 0.004	33.5 ± 4.9	62.1 ± 6.9	438 ± 39
Bermudagrass	Mature	20.9 ± 1.0	10.9 ± 0.9	85.7 ± 7.3	0.034 ± 0.008	30.5 ± 6.4	60.9 ± 7.6	402 ± 78
Crabgrass	Boot	21.6 ± 5.5	12.3 ± 2.4	72.9 ± 6.6	0.042 ± 0.007	24.3 ± 4.4	55.8 ± 13.8	406 ± 132
Crabgrass	Mature	23.0 ± 1.6	13.2 ± 0.9	69.7 ± 3.5	0.042 ± 0.009	24.7 ± 5.6	49.5 ± 5.8	390 ± 97
Crabgrass	Vegetative	21.7 ± 2.1	12.6 ± 1.8	67.5 ± 11.5	0.040 ± 0.007	25.3 ± 4.7	53.6 ± 6.8	424 ± 62
Eastern gamagrass	Boot	22.4 ± 4.3	12.3 ± 2.7	81.1 ± 13.7	0.045 ± 0.018	24.9 ± 8.9	56.2 ± 2.1	466 ± 107
Eastern gamagrass	Early bloom	16.7 ± 2.5	9.7 ± 1.4	84.3 ± 7.6	0.026 ± 0.008	42.4 ± 18.4	73.3 ± 16.9	320 ± 54
Eastern gamagrass	Mature	18.7 ± 4.6	10.3 ± 3.0	89.9 ± 21.9	0.030 ± 0.004	33.8 ± 4.6	65.0 ± 7.9	424 ± 50
Fescue	Early bloom	21.8 ± 5.0	13.8 ± 3.4	57.1 ± 10.4	0.040 ± 0.015	27.5 ± 9.7	53.6 ± 5.4	394 ± 90
Fescue	Mature	16.0 ± 5.9	7.2 ± 2.6	132.3 ± 16.0	0.035 ± 0.006	29.4 ± 5.7	58.9 ± 6.9	535 ± 178
Fescue	Soft Dough	17.8 ± 2.1	9.9 ± 1.7	85.6 ± 14.0	0.043 ± 0.017	25.3 ± 7.7	59.3 ± 6.0	481 ± 109
Caucasian bluestem	Early bloom	20.8 ± 4.5	12.1 ± 2.6	75.2 ± 10.4	0.040 ± 0.014	27.4 ± 9.3	58.8 ± 5.7	371 ± 72
Caucasian bluestem	Late bloom	21.0 ± 3.8	12.7 ± 2.1	67.7 ± 10.3	0.041 ± 0.010	25.7 ± 6.3	55.1 ± 6.8	470 ± 110
Plains bluestem	Early bloom	23.6 ± 5.4	14.7 ± 3.2	59.9 ± 14.4	0.035 ± 0.012	31.4 ± 12.1	60.0 ± 12.6	416 ± 121
Plains bluestem	Late bloom	28.8 ± 2.4	11.1 ± 1.1	78.5 ± 1.9	0.032 ± 0.007	32.7 ± 7.8	62.9 ± 11.4	420 ± 20
Wheat	Dough	22.0 ± 4.0	12.5 ± 2.1	72.2 ± 6.3	0.032 ± 0.002	31.9 ± 2.3	58.2 ± 4.8	518 ± 17
Wheat	Milk	13.6 ± 4.4	7.2 ± 2.2	106.8 ± 9.8	0.030 ± 0.008	35.9 ± 10.7	70.1 ± 14.4	431 ± 121

BW, body weight (kg); MBS, $BW^{0.75}$; DOMI, digestible organic matter intake ($g\,kg\,BW^{-1}$ per day); NDF, neutral detergent fiber.

5–59% of the mean (CV). Average CV across all hays was 21% of the mean.

Weston (1996) proposed that intake of forages could be better understood by separating the demand of the animal from the constraint to meeting that demand imposed by the feed. Competition between the demand to fulfill the theoretical maximum energy capacity and the constraint of the forage that limits fulfilling the theoretical maximum serves as an intake regulator. The constraint to intake is calculated as the difference in quantity of forage that is eaten and the amount expected to be eaten when constraints are absent. For sheep, he used 70 g^{-1} MBS of digestible organic matter intake as the theoretical maximum intake. This constraint was over 100 g kg^{-1} MBS in three grasses (4 weeks bermudagrass, mature fescue and wheat cut in the milk stage) indicating that hay characteristics limited the animal from consuming sufficient quantity to meet its demand. The limiting characteristics could include palatability, bulk density, rate of digestion and passage, rate of comminution by chewing or a variety of other factors.

Passage rate was quite high for several of the grasses (>0.04 g g^{-1} h^{-1}), and consequently, retention time in both the rumen and total gastrointestinal (GI) tract was less for those grasses (Table 3). Rumination time was much higher for grasses than for alfalfa, but several grasses supported fewer ruminating chews per gram of NDF intake (∼20) than the alfalfa (23). Although intuititively we expected retention time and ruminating time to be related, there was little relationship ($r^2 = 0.24$).

3.2. Prediction equations developed from forage chemistry

Organic matter intake as a function of body size was best predicted by forage NDF and the lignin content of NDF (PMLNDF; Table 4). However, the quadratic of NDF produced a statistically better fit than linear. The two variables were selected by the stepwise procedure as the only significant ($P < 0.15$) contributors and accounted for 56% of the variability in intake of this diverse set of forages. The constraint on intake proposed by Weston (1996) was only slightly better predicted than intake per se (also NDF^2 and the reciprocal of PMLNDF). In contrast, the relationship of OMD and the intake constraint was much improved over that of OMD and intake per se (Fig. 2). A single equation could be fit among all forage types, whereas that for intake required one for warm-season perennials and one for all other forages.

Organic matter digestibility was best predicted with NDF^2 and the reciprocal of PMLNDF ($r^2 = 0.54$; Table 4). The reciprocal relationship suggests non-linearity, as does the quadratic. Combining intake and digestibility into a single index (digestible organic matter intake, DOMI) has been proposed as a means to predict animal performance (Raymond, 1969; Heaney, 1970; Mott and Moore, 1970). It is very interesting that with these hays, DOMI could be predicted with greater precision (higher r^2) than either intake or digestibility. However, the residual CV was greater for DOMI (12.2% versus 10.5% for intake and 6.6% for digestibility), suggesting the higher r^2

Table 4
Selected equations for prediction of intake and digestibility using forage chemistry[a]

Y variable	Equation	r^2	S.E.[b]	CV[c]
Organic matter intake (g kg^{-1} BW)	$37.8 - 0.000026 \times NDF^2 - 0.055 \times PMLNDF$	0.56	2.06	10.5
Intake constraint (g OM kg^{-1} MBS)	$53.1 + 0.00018 \times NDF^2 - 5335/PMLNDF$	0.64	12.7	16.0
Organic matter digestibility (g kg^{-1})	$607.6 - 0.00042 \times NDF^2 + 14797/PMLNDF$	0.54	36.9	6.5
Digestible organic matter intake (g kg^{-1} BW)	$15.8 - 0.000022 \times NDF^2 + 583.9/PMLNDF$	0.70	1.39	11.9
Protein digestibility (g kg^{-1})	$829.0 - 26770/CP$	0.89	34.4	6.8
NDF digestibility (g kg^{-1})	$413.7 + 9652/PML$	0.17	46.9	8.3
ADF digestibility (g kg^{-1})	$455.4 + 12394/PMLNDF$	0.20	46.1	7.9

BW, animal body weight; MBS, metabolic body size ($BW^{0.75}$); NDF, neutral detergent fiber; PMLNDF, permanganate lignin in NDF; CP, crude protein; PML, permanganate lignin in dry matter; ADF, acid detergent fiber.

[a] Twenty forage × maturity types were used (see Table 1 for description and chemical composition).

[b] S.E., residual standard error.

[c] CV, residual coefficient of variation.

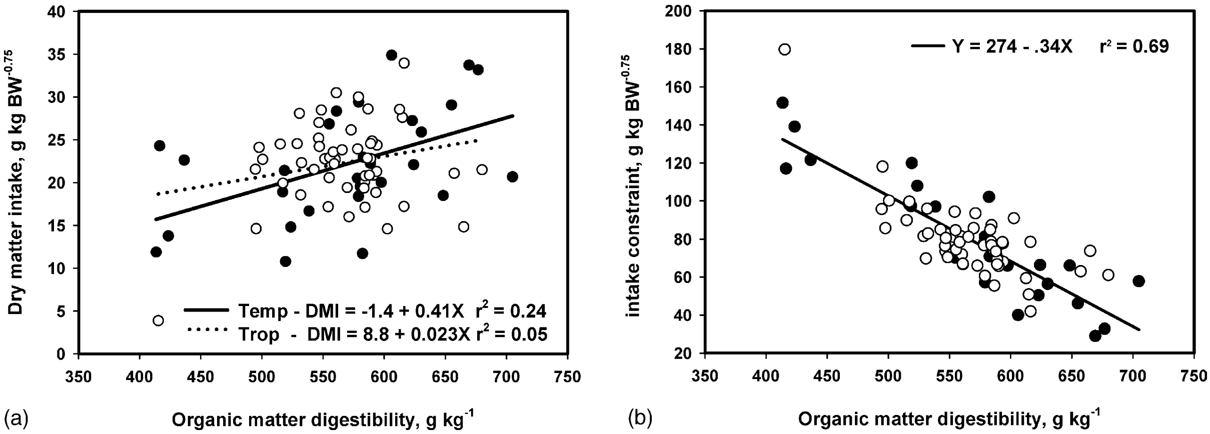

Fig. 2. Relationship of intake (a) or intake constraint (b) to organic matter digestibility of temperate grasses and legumes (●) or tropical grasses (○).

resulted from a greater relative range in DOMI than for either of its components.

Crude protein content was most important for predicting protein digestibility, and the equation was significantly enhanced by the use of the reciprocal term. Since both CP and neutral detergent solubles were uniformly digestible (see Fig. 1 for protein) and therefore were ideal nutritive entities (Lucas Jr. et al., 1961), most of the variability in organic matter digestibility occurred in the cell wall portion. Neither NDF (cell wall; $r^2 = 0.17$) nor ADF (more lignified cell wall material; $r^2 = 0.20$) digestibility could be accurately predicted with forage chemistry. Lignin, either as a proportion of the dry matter (for predicting NDF digestibility) or of NDF (for predicting ADF digestibility), was the selected variable for both. This inability may address the difficulty of accurately predicting in vivo digestibility of forages across a broad range of types (i.e. legumes and grasses).

3.3. Prediction equations developed with ruminating and retention time

The equations for predicting intake using ruminating and retention time (Table 5) were generally improved over those using chemistry (Table 4). The single most important, and only significant, variable selected was the reciprocal of mean retention

Table 5
Selected equations for prediction of intake and digestibility using chewing time and passage parameters[a]

Y variable	Equation	r^2	S.E.[b]	CV[c]
Organic matter intake (g kg^{-1} BW)	$-1.0 + 1227/\text{TMRT}$	0.70	1.65	8.1
Intake constraint (g OM kg^{-1} MBS)	$295.9 - 5975/\text{TMRT} - 0.69 \times \text{CHEW} + 0.00094 \times \text{CHEW}^2$	0.75	10.9	13.7
Organic matter digestibility (g kg^{-1})	$841.6 - 0.00064 \times \text{CHEW}^2 - 2.58 \times \text{TMRT}$	0.56	36.0	6.4
Digestible organic matter intake (g kg^{-1} BW)	$-0.88 - 895.6/\text{TMRT} - 0.000016 \times \text{CHEW}^2$	0.73	1.33	11.5
Protein digestibility (g kg^{-1})	$35.0 + 32857/\text{TMRT} - 0.00054 \times \text{CHEW}^2$	0.53	73.8	14.6
NDF digestibility (g kg^{-1})	$189 + 2.22 \times \text{CHEW} - 0.003 \times \text{CHEW}^2$	0.43	40.1	7.1
ADF digestibility (g kg^{-1})	$169 + 2.39 \times \text{CHEW} - 0.003 \times \text{CHEW}^2$	0.43	39.9	6.8

BW, animal body weight; MBS, metabolic body size (BW$^{0.75}$); TMRT, mean retention time through entire gastrointestinal tract; RMRT, ruminal mean retention time; CHEW, time spent chewing per day; NDF, neutral detergent fiber; ADF, acid detergent fiber.

[a] Twenty forage × maturity types were used (see Table 1 for description and chemical composition and Table 3 for chewing time and passage parameters).

[b] S.E., residual standard error.

[c] CV, residual coefficient of variation.

Table 6
Selected equations for prediction of intake and digestibility using forage chemistry, chewing time and passage rate[a]

Y variable	Equation	r^2	S.E.[b]	CV[c]
Organic matter intake ($\mathrm{g\,kg^{-1}}$ BW)	$3.14 + 1031/\mathrm{TMRT} + 404.3/\mathrm{ADF} - 0.00003 \times \mathrm{ADF}^2$	0.82	1.35	6.68
Intake constraint ($\mathrm{g\,OM\,kg^{-1}}$ MBS)	$129.2 + 0.00012 \times \mathrm{NDF}^2 + 5424/\mathrm{PMLNDF} - 0.58 \times \mathrm{CHEW} + 0.00082 \times \mathrm{CHEW}^2 + 0.72 \times \mathrm{TMRT}$	0.94	5.71	7.19
Organic matter digestibility ($\mathrm{g\,kg^{-1}}$)	$536.0 + 12614/\mathrm{PML} - 0.00065 \times \mathrm{CHEW}^2 - 0.012 \times \mathrm{TMRT}^2$	0.81	24.1	4.24
Digestible organic matter intake ($\mathrm{g\,kg^{-1}}$ BW)	$-10.5 - 0.000013 \times \mathrm{ADF}^2 - 378.5/\mathrm{PML} + 628.8/\mathrm{TMRT} + 0.047 \times \mathrm{CHEW} - 0.000065 \times \mathrm{CHEW}^2$	0.90	0.85	7.61
Protein digestibility ($\mathrm{g\,kg^{-1}}$)	$829.0 - 26770/\mathrm{CP}$	0.89	34.4	6.80
NDF digestibility ($\mathrm{g\,kg^{-1}}$)	$546.6 - 0.00079 \times \mathrm{CHEW}^2 + 19706/\mathrm{PMLNDF} - 0.011 \times \mathrm{TMRT}^2$	0.72	30.7	5.44
ADF digestibility ($\mathrm{g\,kg^{-1}}$)	$137.8 + 1.86 \times \mathrm{CHEW} - 0.0028 \times \mathrm{CHEW}^2 + 17353/\mathrm{PMLNDF}$	0.77	26.0	4.43

BW, animal body weight; MBS, metabolic body size ($\mathrm{BW}^{0.75}$); TMRT, mean retention time through entire gastrointestinal tract; ADF, acid detergent fiber; NDF, neutral detergent fiber; PML, permanganate lignin in dry matter; CHEW, time spent chewing in 24 h; PMLNDF, permanganate lignin in NDF; CP, crude protein.

[a] Twenty forage × maturity types were used (see Tables 1–3 for description and variables).

[b] S.E., residual standard error.

[c] CV, residual coefficient of variation.

time through the entire GI tract (TMRT; $r^2 = 0.70$). The relationship of intake constraint was greater ($r^2 = 0.75$) to ruminating and retention time than to intake ($r^2 = 0.70$), but residual CV was smaller for intake (CV = 8.2%) than for intake constraint (CV = 13.7%). One might expect a closer relationship of ruminating to the constraint of intake, because it is assumed to be a measure of the resistance to particle size reduction and passage of undigested residues.

Equations for prediction of organic matter digestibility using ruminating time (CHEW^2) and TMRT was slightly more precise ($r^2 = 0.56$, S.E. = 36.0; Table 5) than when chemistry was used ($r^2 = 0.54$, S.E. = 36.9; Table 4). The reciprocal of TMRT and the quadratic expressions of RUM were selected to predict DOMI (Table 5). This equation was a slight improvement ($r^2 = 0.73$ versus 0.70) over the equation developed with forage chemistry alone (Table 4). Crude protein, ADF and NDF digestibility were poorly related to ruminating and retention times, although equations for predicting digestibility of ADF and NDF were improved over those using only chemistry.

3.4. Equation development using all variables

Including a combination of chemistry, ruminating and residence time produced a marked improvement in equations for all measures of intake and digestibility (Table 6) except for CP digestibility, for which ruminating or passage information provided no improvement. The constraint on intake was highly related ($r^2 = 0.94$) to descriptions of forage fiber and to ruminating and residence time. The r^2 for ADF digestibility was increased to 0.77, and that for NDF digestibility to 0.72. Residual CV for both NDF and ADF digestibility was quite low and may represent the extent possible for predicting their digestibility, especially considering the high S.D. among animals for individual hays (S.D. for NDF digestibility ranged from 42 to 103; Table 2).

4. Discussion

Variation among animals for OMD (average 5.2% CV) was similar to that reported by others (Minson, 1990; Van Soest, 1982). Variability in intake was greater than that suggested by Minson (1990), but within the range compiled for many different types of forage. Chemical composition and nutrient digestibility varied among hays as expected, with legumes supporting highest nutritive value and grasses the lowest.

Passage rates and total mean retention time for the hays ranged from $0.025\,\mathrm{g\,g^{-1}\,h^{-1}}$ and 86.7 h for a young bermudagrass (poorly consumed) to $0.047\,\mathrm{g\,g^{-1}\,h^{-1}}$ and 22.1 h for the prebloom alfalfa and were generally slower than those reported by Huston et al. (1986) for deer, sheep or goats consuming sorghum (*Sorghum bicolor* (L.) Moench) hay, a warm season annual with similar OMD of many of the hays in the current study. They reported that OMD was higher and rate of passage was lower for goats than for sheep or deer. However, in another experiment, Huston et al. (1986) reported faster passage rate in goats grazing native range herbage than that for either sheep or cattle, and much faster than for all hays in the current study. The faster passage rate was accompanied with reduced digestibility (Huston et al., 1986). Poppi and Minson (1980) noted that cattle digest forage more efficiently than do sheep when forage is offered ad libitum, likely due to slower passage rate from the rumen. Even so, there was little difference in total mean retention time, because hindgut passage was faster for cattle. Reid et al. (1990) reported greater intake by cattle than by goats and sheep, and greater digestibility by cattle and goats than by sheep. The cattle also had slower passage rates than either sheep or goats, and is probably the mechanism for greater digestibility by cattle than for sheep; however, goats apparently are more efficient at digestion than sheep at the same passage rate. The patterns among animal species were similar for all forage types (Reid et al., 1990), unlike the data reported by Silanikove (1986) in which Bedouin goats were more efficient digesters of low quality forage then Saanen milk goats. The data of Reid et al. (1990) would suggest that microbial efficiency may be better in goats than in sheep, but Huston et al. (1986) found inconsistencies in the potency of ruminal fluid from cattle, sheep, goat and deer for in vitro digestibility of four forage types.

Retention time was not different between sheep and goats fed hays of different digestibility (Hadjigeorgiou et al., 2001) and all values were between the extremes observed in the current data. Silanikove (1986) reported an interaction between forage quality (alfalfa versus wheat straw) and goat type (Black Bedouin versus Swiss Saanen) for intake and cellulose digestibility. Bedouin goats supported higher digestibility of dry matter than Saanen goats for all forages, but the difference was greater with medium or low digestibility forage. The Alpine goats of the current study are probably more like the Saanen goats used by Silanikove (1986), both having higher requirements for digestible energy to support milk production. Apparently the Bedouin goats are better adapted for survival strategies, and can better utilize lower quality forage. Likewise, Barbados blackbelly sheep had slower rates of passage than dorset or crossbred sheep, even though intake and digestibility were similar (Mann et al., 1987). However, Hadjigeorgiou et al. (2001) reported that goats supported lower digestibility of N, NDF and OM than sheep. It should be noted that comparisons of passage rate among experiments is somewhat difficult due to differences in markers (Coleman et al., 1984; Burns et al., 1997) and models (Moore et al., 1992). Huston et al. (1986) noted that digestibility of the ruminant diet is partially regulated by ruminal turnover rates and not solely a characteristic of the consumed diet. However, while it is widely recognized that intake and passage rate are related, it is unknown which is the causative agent. Huston et al. (1986) noted that rate factors differ among animal species and probably are important for determining adaptability to habitat. Animals such as Bedouin goats and Barbados sheep that are adapted to feed resources that are either less abundant or lower in quality than herbage found in more temperate regions appear to be able to subsist on lower intakes of digestible energy than animals adapted to the temperate regions.

Metabolic fecal protein (29 $g\,kg^{-1}$ DM intake) is within the values (16–37 $g\,kg^{-1}$) compiled for sheep and goats by Van Soest (1982) and lower than the mean of 47 $g\,kg^{-1}$ from a variety of trials reported by Swanson (1980). Swanson (1980) argued for reporting MFP as a proportion of fecal dry matter rather than intake dry matter. If the average MFP (29 $g\,kg^{-1}$) were subtracted from the fecal CP, then true indigestible protein of the hays can be calculated (Table 2). The values generally increased with increased hay CP content for the grasses and varied (4–20 $g\,kg^{-1}$ DM intake) about the mean of 13.7 $g\,kg^{-1}$. Truly indigestible CP of alfalfa hay was quite higher (28–30 $g\,kg^{-1}$). When protein content of hay was low, the larger ratio of MFP to undigested hay protein contributed to the low apparent protein digestibility as in mature Eastern gamagrass and fescue since the CP content in those hays was very low ($<$70 $g\,kg^{-1}$).

Typical relationships were found between nutritive potential and forage chemistry. Forage chemistry accounted for about 55% of the variation in both intake and OMD across forages in goats. Forage quality analyses almost always include determinations of CP, NDF, and ADF. Within forage species these values vary in a consistent manner and may be used to rank quality. Rohweder et al. (1978) found that correlations between intake and NDF concentration lacked consistency and were generally low for subtropical species. Different equations relating intake to NDF were proposed for legumes and grasses. Mertens (1973) found that 49% of the variation in intake of a wide array of forages over several locations could be explained by NDF content of the forages. Moore et al. (1996) used CP, ADF and NDF with all squares and interactions to develop equations for predicting both intake and digestibility across a divergent variety of forages. However, in vitro digestibility was a dominant entity in predicting in vivo digestibility, and has been used routinely in screening forage breeding experiments since its development in the 1970s. In the current study, digestible CP was closely related to protein content because CP behaves as an ideal nutritive entity (Lucas Jr. et al., 1961; Van Soest, 1965).

Intake was better related to measures of resistance to breakdown (ruminating and retention time) than simple measures of forage chemistry. Welch and Smith (1969) demonstrated a high correlation of rumination time to NDF intake. Other reports have addressed the relationship of ruminating time and either intake or particle size reduction (Welch, 1982; Lee and Pearce, 1984; Kennedy, 1985). Reid et al. (1990) noted that intake was correlated ($r^2 = -0.41$; $P < 0.05$) with mean retention time for goats, but not for sheep and cattle. Luginbuhl et al. (1989) stated that ingestive mastication was a highly efficient process, but that the proportion of particles collected at the esophagus of cattle that were retained on a 4 mm sieve decreased linearly with increased level of intake of the same hay. This would suggest that at higher levels of intake, greater rumination time would be necessary to reduce the particles to passage size and density. Current theory is that rumen space, and thus intake, is limited by undigested feed residue in the rumen. As residue particles are degraded by digestion and mastication so that they are sufficiently small and dense, they exit the rumen. If a decline in forage quality through maturity requires increased need for remastication to reduce the particle size, the rumination time per unit of forage ingested should increase, and may limit its intake (Welch and Smith, 1969). Therefore, rate and degree of particle size reduction through chewing and microbial digestion form a fundamental constraint to increased intake. Alternatively, Hadjigeorgiou et al. (2001) noted that goats exhibited a greater degree of selection than sheep when fed ad libitum which resulted in greater intake and a diet of smaller particles, with no subsequent effect on digestibility or passage rate. Perhaps the ability or desire for selectivity partially substitutes for the need to remasticate ruminal residues, though they did not report rumination times. Attempts to model intake based on passage and digestion rates (i.e. Waldo et al., 1972) could be improved with information on the quantitative relationships between mastication (both eating and ruminating) and particle size reduction.

While the use of rumination time and passage rate do not provide easily determined measures for use in calibration and prediction of in vivo intake and digestibility, it does provide some insight on what is important for these relationships across a rather broad collection of forage types. Various attempts have been made to mimic rumination using mechanical devices such as artificial mastication (Troelson and Bigsby, 1964), grinding energy (Minson and Cowper, 1974), and compression/fragility measurements (Baker et al., 1993; Henry et al., 1996, 1997). These data suggest that the search for a rapid, reliable and easily determined measure of the toughness and fragility of forages should not cease but that some method of screening breeding material for these characteristics is merited. Databases on which ruminating and passage data along with in vivo animal measurements are sorely needed for validation of these relationships and to develop methods that are easy to obtain and that are useful for comparing, ranking, and eventually predicting quality of individual forages.

While digestibility has been used to predict intake (Freer and Jones, 1984), Moore and Coleman (2001) reported a wide range of correlations between intake and digestibility and suggested that digestibility is not a reliable predictor of intake. It does appear from this diverse group of forages that the relationship of digestibility to intake constraint may be more precise than that for digestibility (Fig. 2), but care must be taken with this interpretation since digestibility is a part of the calculation of the intake constraint.

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